Turtles (Reptilia: Testudines) Of The Ardis Local Fauna Late Pleistocene (Rancholabrean) Of South Carolina

Curtis C. Bentley and James L. Knight
South Carolina State Museum, 301 Gervais Street,
P.O. Box 100107
Columbia, South Carolina 29202-3107

ABSTRACT- The Ardis local fauna (late Pleistocene) was collected from a group of interconnecting sediment-filled solution cavities, located in the Giant Cement Quarry near Harleyville, Dorchester County, South Carolina. Fossil material from the lowermost levels and the extreme upper layer of the deposit have been radiocarbon dated at 18,940 ± 760 and 18,530 ± 725 y.b.p., respectively. These dates are considered contemporaneous within present resolution. Approximately ninety vertebrate taxa were collected from the site. Fourteen were species of turtles, including eight not previously reported from the Pleistocene of South Carolina. Among these is the southeasternmost occurrence of *Emydoidea blandingii.* This record, in conjunction with other vertebrate fossils from the site, suggests a north-south dispersal route of species along the Atlantic Coastal Plain during interglacial-glacial transitions. Geographically isolated eastern and western populations of *Emydoidea blandingii* may have existed during the maximum advance of the Laurentide ice sheet. Unusually complete fossils of large box turtles recovered from the site corroborate the previously suggested synonymy of the extinct *Terrapene carolina putnami* with *T. c. major.* The fossil turtle community of the Ardis local fauna has no modern analogue. Like the Ardis mammals, it comprises a "disharmonious" fauna which suggests that, during the height of the Wisconsinan glaciation, the region experienced a more equable climate than that of today .

The Ardis local fauna has yielded approximately 90 species of late Pleistocene fossil vertebrates from the Coastal Plain of South Carolina, including a substantial mammalian (Bentley et al. 1994), avian, reptilian, amphibian, and fish faunas currently under study. We present data on the Ardis turtle collection (Appendix I), the largest Rancholabrean fauna reported from the state. Dobie and Jackson (1979) and Roth and Laerm (1980) reported fossils of late Pleistocene age from Edisto Island, the only other Pleistocene fossil turtle fauna from South Carolina described to date. Among the Edisto Island fauna were ten

taxa of turtles, including *Gopherus* sp. and *Malaclemys terrapin* which were not recovered from the Ardis local fauna and possibly three species of *Pseudemys, P. floridana* and/or *P. concinna*, and *P. nelsoni.*

The Ardis local fauna was discovered in a large open-pit mine, operated by the Giant Cement Company, located 5 km NNE of Harleyville, Dorchester County, South Carolina (33° 14'N, 80° 26'W). Quarry operations exposed Santee Limestone (middle Eocene) and the clay-rich Harleyville Formation (late Eocene) which underlie Plio-Pleistocene surficial deposits (Ward et al. 1979, Harris and Zullo 1991). Locally, groundwater differentially dissolved the Santee Limestone in its upper portions, so that many solution cavities contacted and penetrated the overlying Harleyville Formation and thereby opened several of the cavities to the Pleistocene surface (Bentley et al, 1994). The radiocarbon dates of the Ardis material place the time of deposition at or near the height of the Wisconsinan glaciation (Bowen 1988, Tushingham and Peltier 1993). Further discussion on the geology, dating methods of the Ardis fossil material, previous fossil collections from the quarry, fossil collection procedures, and a locality map are available in prior publications (Bentley and Knight 1993, Bentley et al. 1994).

TAPHONOMY

At least part of the fossil assemblage collected from inside the solution cavities at the Ardis site appears to represent an obrution deposit, the very rapid burial of intact organisms (Brett 1990) in which many of the specimens exhibit incipient decay. Surface openings leading to the cavities varied from a gentle downward slope to a vertical shaft, generally allowing the Pleistocene fauna ease of ingress and egress. This permitted animals to enter the cavities in three different ways: (1) "walk-in" taxa, which may have used the site for estivation/hibernation or as denning sites and hunting grounds, for example muskrats, mink, and woodrats (Bentley et al. 1994); (2) "wash-in" taxa from the surface, either alive or dead, which applies most readily to large animals known only from isolated remains e.g., *Mammut* sp., *Bison* sp., *Equus* sp. (Bentley et al. 1994), that would have been unable to enter the cavities during life; and (3) "fall-in" taxa which fell into exposed verticle shafts, fossil accumulations resulting from this type of natural trap are well documented (e.g., Webb 1974).

Because of the interconnecting "tunnel-like" nature of the cavities, a single episodic event could produce differing water velocities within the cavities and different rates of deposition. Seasonal flooding, depending on the intensity, may have simultaneously smothered living animals within the cavities and buried or reworked those that had died just prior to, or in a preceding, depositional event. Consequently, specimens incompletely or shallowly buried during an event with a low sedimentation rate (low energy) could be completely or partially exhumed and reburied by a succeeding event. This resulted in the preser-

vation of specimens in various orientations to the bedding planes (Fig. 1), various degrees of disarticulation, and the occasional mixing of individual elements. An articulated *Emydoidea blandingii* specimen preserved in its life position with axial skeletal elements inside, indicates little or no decay prior to its final burial (Fig. 2). This preservation suggests the turtle was buried quickly in a high energy, high sedimentation environment (Brett and Speyer 1990), resulting in burial deep enough to avoid reworking during subsequent episodic events. Several articulated turtles were collected with limbs and skulls preserved within the shells in various orientations to the bedding plane. A high energy hydrological environment before or shortly after death would likely explain the various orientations observed in well preserved specimens. Retention and preservation of limb elements, cervical and caudal vertebrae, and skulls inside the shell may reflect a withdrawal by the turtles in response to a catastrophic event.

Fig. 1 *Emydoidea blandingii,* only the carapace (.547) was preserved, ventral side up (side view), among clay clasts from the surrounding Harleyville Formation. This illustrates the hydrodynamic effect upon some specimens prior to final burial.

Fig. 2 Complete *E. blandingii* (.546) *in situ*, with axial skeleton preserved inside the shell, indicating a "withdrawal response" and final burial prior to any significant decay.

MATERIALS AND METHODS

Morphological terminology used in this paper is taken from Carr (1952), Ernst and Barbour (1989), Holman (1967, 1977, 1985), Holman and Grady (1987), and Preston (1979). Taxonomy follows Conant and Collins (1991).

Morphological comparisons of Recent skeletons to fossil material were made against available specimens in the Florida Museum of Natural History and the South Carolina State Museum collections. Additionally, specimens from The University of Michigan Museum of Zoology of *Emydoidea blandingii*, UMMZ 155047-155054, *Clemmys guttata*, UMMZ 51235, 51236, 51240-51242, 159219, 155001, 155002, and *Clemmys muhlenbergii*, UMMZ 77140 and, 130840 were studied.

Most of the specimens in the South Carolina State Museum collections are deposited under the base number of S.C. 94.10. and for brevity, are referenced in the text only by the digits following this base number. Specimens accessioned separately are designated by the institutional prefix of SCSM. Fossil specimens deposited in the National Museum of Natural History and the Florida Museum of Natural History are designated by USNM and UF, respectively.

SYSTEMATIC PALEONTOLOGY

Testudines

Kinosternidae

Material: 1 right xiphiplastron (.25); 16 peripherals (.26-.44); 2 humeri (.45-.46); 2 partial jaw rami (.755-.756).

Remarks: These fossil elements could only be identified with confidence to family.

Kinosternon subrubrum - Eastern Mud turtle (Lacepede, 1788)

Material: 3 nuchals (.11-.13); 2 right, 3 left hyoplastra (.6-.10); 5 left hypoplastra (.1-.5).

Characters used for identification: The hyoplastron of *Kinosternon subrubrum* can be separated from other North American *Kinosternon* and *Sternotherus* because the axillary notch is narrower, and from *Kinosternon baurii* because the axillary notch is wider and shallower (Holman 1985). *K. subrubrum* hyo- and hypoplastra differ from *Sternotherus odoratus* in that the elements are shorter laterally than medially in *S. odoratus* (Preston 1979). Characters used to identify nuchal material are discussed by Holman (1975). In addition, nuchals of *K. subrubrum* can be distinguished from nuchals of *S. odoratus* because the anterior lip of the nuchal, viewed anteriorly, is nearly straight in *K. subrubrum*. Nuchals of *S. odoratus*, viewed anteriorly, have a decided arc.

Remarks: The eastern mud turtle inhabits a variety of shallow slow to non-moving bodies of water with a soft substrate, such as swamps, ponds, marshes, wet meadows, and lagoons (Ernst and Barbour 1989). *Kinosternon subrubrum* today ranges from southern Massachusetts and Pennsylvania along the Atlantic coast, to the tip of Florida and west into Texas and Oklahoma (Conant and Collins 1991). *K. subrubrum* is common in the area of the Ardis site today and may be sympatric with *K. baurii* (Lamb and Lovich 1990).

This is the first report of this species from the fossil record of South Carolina. Dobie and Jackson (1979) and Roth and Laerm (1980) both reported the same single pygal bone from Edisto Island as "*Kinosternon* sp."

Sternotherus odoratus - Common Musk turtle (Latreille, in Sonnini and Latreille, 1802)

Material: 3 nuchals (.22-.24); 2 right hyoplastra (.14-.15); 1 right, 5 left hypoplastra (.16-.21).
Characters used for identification: Identification is based on characters provided in discussion for *Kinosternon subrubrum*. The hyo-hypoplastron of *S. minor* can be separated from the same elements in *S. odoratus* because the area that forms the bridge between the plastron and the carapace is dorsally compressed or flattened in *S. minor*, and not raised as in *S. odoratus*. The nuchals compare most favorably to *S. odoratus*, following the characters used above, and additionally exhibit a strong dorsal medial keel that is generally lacking in *K. subrubrum*.

Remarks: The common musk turtle inhabits areas very similar to that of *K. subrubrum*, preferring slow to non-moving bodies of water with a soft bottom. It has also been collected from fast moving, gravel bottomed, streams (Ernst and Barbour 1989). *S. odoratus* occurs from southern Maine and Canada southward through Florida and as far west as Kansas and central Texas (Conant and Collins 1991), and occurs in the area of the Ardis site today.

Chelydridae
Chelydra serpentina - Snapping turtle (Linnaeus, 1758)

Material: 2 right parietals (.50, .53); 1 left postorbital (.51); 1 right prefrontal (.52); 1 left quadratojugal (.54); 1 partial left mandible (.55); 2 right mandibles (.56-.57); 6 cervical vertebrae (.102-.107); 1 humerus (.63); 2 radii (.69-.70); 1 right scapulo-acromial process (.64); 1 right partial acromial process (.65); 5 femora (.58-.62); 3 ilia (.66-.68); 1 caudal vertebra (.108); 1 nuchal (.95); 1 right 1st peripheral (.71); 16 unassigned peripherals (.72-.83)(2 USNM)(2 UF); 1 left 1st costal (.84); 24 partial costals (.85-.92)(8 USNM)(8 UF); 2 associated costals (.93-.94); 2 neurals (.96-.97); 2 epiplastra (.100-.101); 2 hypoplastra (.98-.99).

Characters used for identification: *Chelydra* shell material is very distinctive and easily separated from other turtles including *Macroclemys*. Preston (1979) provides characters that allow the identification of fragmentary material. All listed fossil elements compare favorably to Recent skeletal materials.

Axial and appendicular skeleton - The large size and diagnostic ornamentation of the *Chelydra* skull roof elements distinguish them from all other turtles. *Macroclemys* lacks the rugose cranial ornamentation of *Chelydra*. A pectoral girdle was assigned to this species based on the 90° angle between the scapula and acromial process and on the heavily striated distal ends (Holman 1966). Femora and humeri could not be separated from Recent material of *C. serpentina*, and are more robust than other genera of fresh water turtles (Holman 1964) except *Macroclemys*, which is generally considerably larger.

Remarks: Snapping turtles are generally found in freshwater to brackish water habitats with soft muddy substrate (Ernst and Barbour 1989) from eastern Canada through the United States east of the Rockies south through Mexico and into Ecuador. *C. serpentina* occurs today in the Ardis area.

Dobie and Jackson (1979), first reported fossil material of *C. serpentina* from Edisto Island with additional material reported by Roth and Laerm (1980).

Macroclemys temminckii - Alligator snapping turtle (Gray, 1855)

Material: 1 partial right parietal (.109).

Characters used for identification: The fossil parietal is identical to Recent specimens of this turtle, differing from *C. serpentina* in that the dorsal surface is smooth, i.e. without any of the prominent ornamentation consistently found in *C. serpentina* (Fig. 3). The parietal of *M. temminckii* is generally more robust and is longer with respect to width than specimens of *C. serpentina* of comparable sizes. This was the only fossil element of this species collected from the site. Because this represents a significant range extension, assignment to this species was made only after exhaustive comparisons to the fossil and Recent collections at the Florida Museum of Natural History and the South Carolina State Museum negated all other possibilities.

Remarks: This is the largest freshwater turtle in North America and possibly the heaviest in the world (Ernst and Barbour 1989). The alligator snapping turtle often can be found in the deep waters of lakes, ponds, rivers and bayous that contain abundant aquatic vegetation and muddy bottoms. This turtle is highly aquatic and ranges westward from northern Florida into Texas along the Gulf Coast and thence northward up the Mississippi Valley into Illinois, Iowa and Kansas (Ernst and Barbour 1989).

This is the first fossil or Recent evidence of *Macroclemys* from South Carolina and the Atlantic Coastal Plain.

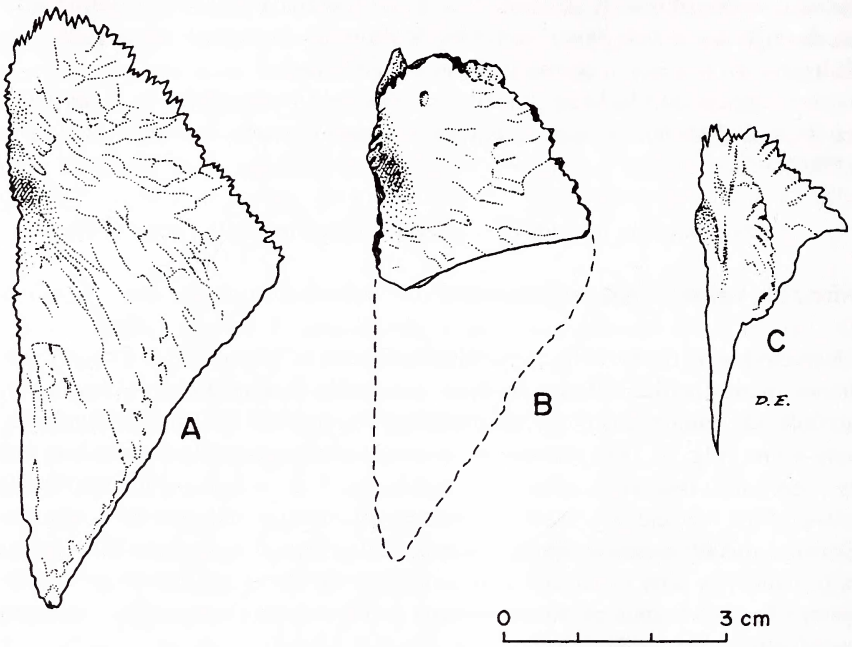
Emydidae

Emydinae

Chrysemys picta - Painted turtle (Schneider, 1783)

Material: An individual specimen consisting of a complete carapace (missing the 3rd right marginal) and plastron (.110); 7 cervical vertebrae (.110.1-.110.7); 1 ulna (.110.16); 1 radius (.110.17); 4 phalanges (.110.18-.110.21); 1 ungual (.110.22); 2 partial scapulo-acromial processes (.110.11-.110.12); 2 coracoids

Fig. 3 Right parietals of *Macroclemys temminckii* and *Chelydra serpentina*. A) Recent *M. temminckii*. B) Ardis fossil. C) Recent *C. serpentina*.



(.110.13-.110.14); 2 dorsal vertebrae (.110.9-.110.10); complete pelvic girdle (.110.15); 1 caudal vertebra (.110.8). An individual specimen consisting of a nearly complete carapace and plastron (.111). An individual specimen consisting of a complete carapace (missing left 8-9th peripherals and 6th neural) and plastron (.112); partial skull and mandible (.112.1); partial hyoid process (.112.2); 7 cervical vertebrae (.112.20-.112.26); 2 humeri (.112.5-.112.6); 2 ulnae (.112.7-.112.8); 2 radii (.112.9-.112.10); 2 scapulo-acromial processes (.112.15-.112.16); 2 coracoids (.112.17-.112.18); 2 femora (.112.3-.112.4); 2 tibiae (.112.11-.112.12); 2 fibulae (.112.13-.112.14); 7 metapodial elements (.112.42-.112.48); 31 phalanges (.112.49-.112-80); 13 unguals (.112.81-.112.91); 2 sacral ribs (.112.92-.112.93); partial pelvic girdle (.112.19); 3 dorsal vertebrae (.112.27-.112.29); 12 caudal vertebrae (.112.30-.112.41). An individual specimen consisting of a nearly complete plastron and attached 4-7th right peripherals (.113); skull (including inner ear ossicles) and mandible (.113.1); partial hyoid apparatus (.113.2); 4 cervical vertebrae (.113-.9-.113.12); 2 humeri (.113.3-.113.4); 1 scapulo-acromial process (.113.7); 2 partial femora (.113.5-.113.6); 1 tibia (.113.8); 2 metapodial elements (.113.15-.113.16); 15 phalanges (.113.17-.113.31); 5 unguals (113.32-.113.36); 2 caudal vertebrae (.113.13-.113.14). Specimen with partial carapace (.114); 3 cervical vertebrae (.114.3-.114.6); 1

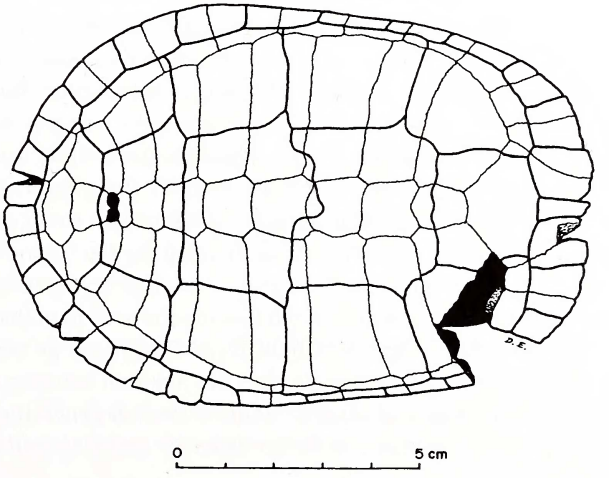
humerus (.114.1); 1 radius (.114.2); 1 phalange (.114.7). 2 mixed specimens both with partial fragmented carapaces and plastra (.115); 3 cervical vertebrae (.115.5-.115.6); 2 humeri (.115.1-.115.2); 2 scapulo-acromial processes (.115.3-.113.4); 2 coracoids (.115.8-.115.9); 2 tibiae (.115.10-.115.11); 1 ilium (.115.12); 1 phalange (.115.13). Four individual specimens with fragmented carapace and plastron (.116-.119). Two mixed specimens with badly fragmented carapaces and plastra (.120).

Isolated elements: 16 nuchals (.123-.132)(3 USNM)(3 UF); (SCSM 91.170.1) partial plastron; 10 right and 2 left epiplastra (.133-.144); 2 entoplastra (.169-.170); 10 left and 3 right hyoplastra (.145-.151)(3 USNM)(3 UF); 1 right hypoplastron and xiphiplastron (.122); 5 left and 7 right hypoplastra (.152-.157)(3 USNM)(3 UF); 6 left and 9 right xiphiplastra (.158-.168)(2 USNM)(2 UF); 8 right and 6 left 2nd costals (.227-.240); 3 right and 1 left 3rd costals (.241-.244); 6 right and 3 left 4th costals (.245-.253); 7 right and 8 left 5th costals (.254-.268); 4 right and 3 left 6th costal (.269-.275); 4 right and 1 left 7th costal (.276-.280); 56 peripherals (.171-.226); 1 mandible (.761); 2 right and 1 left mandibular rami (.758-.760); 10 humeri (.289-.298); 8 femora (.281-.288).

Characters used for identification: Identification of complete shells was based on nuchal characters (Bentley and Knight 1993), and the alignment of the vertebral and pleural sulci (Ernst and Barbour 1989) (Fig. 4).

Hyoplastron - The humeral sulcus does not cross dorsally over the plastral scute overlap area, as in *Clemmys*. *Terrapene* and *Emydoidea* have hinged plastra. Elements of comparable size can be separated from *Deirochelys reticularia* as the dorsal scute overlap area in *C. picta* is wider and more sharply curved

Fig. 4 Fossil carapace of *Chrysemys picta* (.110) from the Ardis local fauna.



distally, and the articulating surface of the epiplastron and hyoplastron between the entoplastron and the outside edge is wider in *C. picta*. *Trachemys* and *Pseudemys* are larger and more robust than *C. picta* as adults. Young specimens of *Trachemys* and *Pseudemys* can be separated by a less pronounced or inflated scute overlap area and signs of incomplete ossification.

Hypoplastron - The inguinal sulcus runs diagonally to the peripherals and into the inguinal notch in *Chrysemys* but is parallel to the peripherals in *Clemmys*. This element can be distinguished from *Deirochelys* as it is less elongate with respect to width in *C. picta*, and the scute overlap area is wider. It can also be separated from *Terrapene carolina* and *Emydoidea* by the lack of a hinge. Adult *Trachemys* and *Pseudemys* differ in being larger and more robust than adults of *C. picta*. Young specimens of *Trachemys*, comparable in size to adult *C. picta* and completely ossified, can be separated from *C. picta* by a larger bridge with respect to the hypoplastron proper and a greatly reduced or absent epidermal attachment scar.

Entoplastron - The humero-pectoral sulcus does not cross the entoplastron as in eastern species of *Clemmys* and in *Terrapene carolina*. It can be tentatively separated from *Pseudemys*, *Trachemys*, and *Emydoidea* by overall size, as specimens of the preceding genera tend to exhibit incomplete ossification when of comparable size to adult *C. picta*. However, size alone is not a reliable character for this element. We were unable to separate this element from that of *Deirochelys*, so entoplastra are only tentatively assigned to *C. picta*.

Epiplastron - This element differs from other species (except *Trachemys*) in that the anterior edge exhibits a degree of serration. This element often is serrated in specimens of *Trachemys*, but the size of these specimens allows easy separation from *C. picta*. Young specimens of *Trachemys* generally lack this serration and have a poorly developed scute overlap area in comparison to *C. picta* of comparable size.

Xiphiplastron - This element can be separated from *Clemmys*, *Terrapene*, and *Emydoidea* by the scute overlap area, which in those genera is more pronounced than in *C. picta*. Further, *Clemmys muhlenbergii* has a posterior edge tapered to a point, while in *Clemmys insculpta* the element is longer with respect to width, with a pronounced notch where the anal sulcus wraps over the edge, a condition minimal or lacking in *C. picta*. In *C. picta* the scute overlap of this element is wider and more pronounced on the posterior edge than on any examined specimens of *Deirochelys*. This element in *Trachemys* is generally more robust in adult specimens than in *C. picta*, and in young specimens of comparable sizes the scute overlap area is much less pronounced than that of *C. picta*.

2nd Costal - This element differs from *C. guttata* in being approximately 30% wider with respect to length, and the junction between the 2nd vertebral sulcus and the 1st and 2nd pleural sulcus is located generally more distally than in *C. guttata*. This element differs from *C. muhlenbergii* by having a

greater curvature, and the above mentioned junction point forms a distinct "T" shape in *C. muhlenbergii* and dips into a general "U" or "V" shape in *C. picta*. The 2nd costal of *C. picta* differs from *C. insculpta* by being completely smooth and lacking any "tortoise-like" bulges, by being more distally flared, and by having greater curvature of the element. It can be separated from *Trachemys* and *Pseudemys* by a lack of sculpting and smaller size, and from *Deirochelys* by lack of sculpting, a more proximal rib attachment (Jackson 1978), and the proximal tapering of the element.

3rd Costal - Differs from *Clemmys*, *Terrapene*, *Trachemys*, *Pseudemys*, *Emydoidea*, and *Deirochelys* in that it lacks the vertebral sulcus between the 2nd and 3rd vertebral scutes. Additionally, in *Deirochelys* the rib attachment is significantly more distal than in *C. picta*. This 3rd element can be separated from the 5th costal in *C. picta* in that it lacks the posteriorly directed curvature of the 5th costal.

4th Costal - Can be separated from all other emydid turtles in that it exhibits alignment of the sulci between the 2nd and 3rd vertebral and pleural scutes. This sulcal alignment occurs only in the subspecies *C. picta picta* (Conant and Collins 1991).

5th Costal - Can be separated from *Clemmys*, *Trachemys*, *Deirochelys*, *Pseudemys*, *Emydoidea*, and *Terrapene* by characters given for the 3rd costal.

6th Costal - Differs from *Clemmys*, *Trachemys*, *Deirochelys*, *Pseudemys*, *Emydoidea*, and *Terrapene* in that it lacks the sulcus of the 3rd and 4th vertebral scutes.

Peripherals, femora, humeri, and mandibular rami - These elements are tentatively assigned to this species as they compare most favorably to Recent and fossil material of *C. picta*.

Remarks: The painted turtle has a wide distribution, occurring from southern Canada south into Mexico and across the entire continental United States (Ernst and Barbour 1989). Lakes, ponds, and streams are typical habitats of the painted turtle. Slow to non-moving, shallow aquatic environments with soft bottoms are favored.

The completeness of many of the painted turtles recovered from the Ardis site are strong indicators of an obrution deposit. *Chrysemys picta* occurs in the Piedmont and mountains of South Carolina today but does not inhabit the Ardis site or any other part of the Coastal Plain. This is the first fossil record from South Carolina.

Clemmys guttata - Spotted turtle (Schneider, 1792)

Material: An individual specimen consisting of a nearly complete shell (SCSM 93.90.1) missing only the right hypoplastron and xiphiplastron, figured in Bent-

ley and Knight (1993), and the following associated cranial and postcranial elements; articulated skull fragment (prefrontal, frontal, postorbital, parietal, and supraoccipital), right maxilla, both quadrates, both opisthotics, basisphenoid, and articulated lower jaw, 1st cervical vertebra, 2 humeri, 1 ulna, 2 coracoids, 1 ischium, partial pubis and ilium, 1 sacral rib, 1 fibula, 3 phalanges, and vertebrae fragments. An individual specimen consisting of a partial carapace and plastron missing only the left hypoplastron and xiphiplastron (.299). Isolated skull fragment (parietal, supraoccipital, both maxillae, basisphenoid, 1 quadrate, 1 postorbital, 1 partial squamosal) (.299.1). A single sub-adult individual with partial plastron and 2 peripherals (.121.1-.121.2).

Isolated elements: 17 nuchals (SCSM 93.90.2-.8)(5 USNM)(5 UF); 3 right and 2 left 2nd costals (.334-.338); 6 right and 5 left 3rd costals (.339-.349); 6 left and 6 right 4th costals (.350-.361); 3 right and 2 left 5th costals (.362-.366); 7 right and 4 left 6th costals (.367-.377); 1 left 7th costal (.378); 34 peripherals (.300-.333); 5 right and 3 left epiplastra (.379-.386); 3 entoplastra (.417-.419); 5 right and 13 left hyoplastra (.387-.399,.432)(2 USNM)(2 UF); 3 left hypoplastra (.400-.402); 6 right and 10 left xiphiplastra (.403-.416)(1 USNM)(1 UF); 1 mandible (.757); 3 humeri (.426-.428); 6 femora (.420-.425).

Characters used for identification: Identification of the two most complete specimens is discussed by Bentley and Knight (1993).

Nuchals - See Bentley and Knight (1993), for characters used to distinguish this from other possible identifications.

Epiplastron - Differs from *C. picta* in that the scute overlap area is more robust in *C. guttata*, and the anterior edge is not serrated as is common with *C. picta*. It can be separated from *C. muhlenbergii* because the bulbous area where the gular sulcus wraps onto the scute overlap is usually considerably wider medially to laterally in specimens of *C. guttata*, whereas the scute overlap portion that is posterior to the bulbous area is narrower in *C. muhlenbergii* than *C. guttata*. The length of the scute overlap posterior to the gular sulcus is longer than that of *C. picta*. Also, the epidermal attachment scar in *C. muhlenbergii* is deeply incised and tends to undercut the scute overlap area. The epiplastron of *C. guttata* is rarely incised to this extent. The epiplastra of *C. insculpta* differ from *C. guttata* in that the bulbous area where the gular sulcus crosses the dorsal surface is only slightly or not at all bulbous in specimens of similar size. The epiplastron of *Deirochelys*, *Trachemys* and *Pseudemys* that fall within the size range of *C. guttata* have less pronounced scute overlap area compared to that of *C. guttata*. *E. blandingii* specimens of comparable size show sub-adult traits (incomplete ossification) and have a less pronounced scute overlap area. *Terrapene* epiplastra differ in that the area posterior to the scute overlap is concave, forming a depression posteromedially to the gular sulcus, generally absent in *C. guttata*.

Hyoplastron - Differs from *Terrapene* and *Emydoidea* in that *C. guttata* lacks the hinge components. *C. muhlenbergii* differs slightly from *C. guttata* in that the scute overlap is narrower in *C. muhlenbergii*. Specimens of *Trachemys* and *Pseudemys* that fall within the size range of *C. guttata* have scute overlaps that are greatly reduced in comparison to *C. guttata* and the elements exhibit incomplete ossification. *Deirochelys* and *Chrysemys picta* can be separated from *Clemmys guttata* because the distance between the entoplastron and hypoplastron is ca. 40% greater in adults of the former two genera. Also, in *C. picta*, the humeral sulcus does not cross dorsally over the scute overlap area. *C. insculpta* exhibits incomplete ossification when elements fall within the size range of *C. guttata*.

Hypoplastron - This element can be separated from other genera of emydid turtles by the lack of hinge components (separating it from *Terrapene* and *Emydoidea*), or by its posterior width being greater than its length (separates it from *Trachemys* and *Pseudemys*). Holman (1977) gives characters used to separate this element from *C. muhlenbergii* and *C. insculpta*.

Xiphiplastron - Separation of this element from *C. picta* is listed under that species. It can be separated from *C. muhlenbergii* and *C. insculpta* in that the posterior edge is generally squared off rather than tapering to a point, as in the other two species. However, some specimens of *C. guttata* do exhibit a pointed condition. These still can be separated from *C. muhlenbergii* because the area where the abdominal muscle attaches to the xiphiplastron is more pronounced. *C. insculpta* can also be separated from *C. guttata* because, in the area where the anal sulcus crosses onto the scute overlap area, the xiphiplastron is deeply notched, being greatly reduced or lacking in *C. guttata*.

Entoplastron - In *C. guttata* the humero-pectoral sulcus crosses the entoplastron within the anterior half of that element. In *C. muhlenbergii* the humero-pectoral sulcus may cross the entoplastron at its posterior extremity, but typically it does not cross the entoplastron at all (Bentley and Knight 1993). These fossil entoplastra are tentatively assigned to *C. guttata*, and not *C. insculpta*, because this element is generally more robust in *C. insculpta* and the humero-pectoral sulcus crosses the entoplastron more posteriorly in *C. insculpta* than in *C. guttata*.

Costal - Characters used to differentiate costal elements from *C. picta* are described in that section. Costals of *Clemmys guttata* differ from *C. muhlenbergii* in having substantially more curvature. The dorsal surface of costals in *C. guttata* is smooth, lacking any exterior bulges or sculpturing common to adult *C. muhlenbergii*, *C. insculpta*, *Deirochelys*, *Trachemys*, and *Pseudemys*. The costals of *Emydoidea*, *Trachemys*, and *Pseudemys* exhibit immature traits when they are within the size range of *C. guttata*. *Terrapene* has deeply incised sulci, and its elements tend to be more acutely angled proximally and exhibit "bulbous" sculpturing.

Peripherals, femora, humeri, and mandible - These elements are tentatively referred to this species because they compare most closely to Recent and fossil *C. guttata*.

Remarks: The spotted turtle ranges from northern Illinois into Ohio and Ontario, east to Maine and New York, and south along the Atlantic Coastal Plain into northern Florida (Conant and Collins 1991). *Clemmys guttata* occurs most commonly in bogs or marshy pastures, but it also can be found in woodland streams. It favors habitats with soft substrates. *C. guttata* is frequently found away from water, but even so it is the least terrestrial of the three eastern species of *Clemmys* (Ernst and Barbour 1989). The fossil spotted turtle remains from the Ardis local fauna represent the oldest known material of this species (Bentley and Knight 1993), and the first fossil record for the eastern United States. Holman (1990) reports a right epiplastron from a 6,000-year-old fauna near Lansing, Michigan. Interestingly, Ernst and Barbour (1989) noted a relationship between this turtle and the burrows of muskrats, which the turtles apparently use for estivation and hibernation sites. Fossil muskrats were the most common mammals found at the Ardis site (Bentley et al. 1994) and are believed to have used the solution cavities as burrow sites. This may help to explain the abundance of this turtle at the Ardis site.

Clemmys muhlenbergii - Bog turtle (Schoepff, 1801)

Material: An individual consisting of a partial carapace (nuchal, 1st and 2nd left costals and peripherals, 2 peripherals, numerous shell fragments) and plastron (both epiplastra, and partial hyoplastron) (.429).

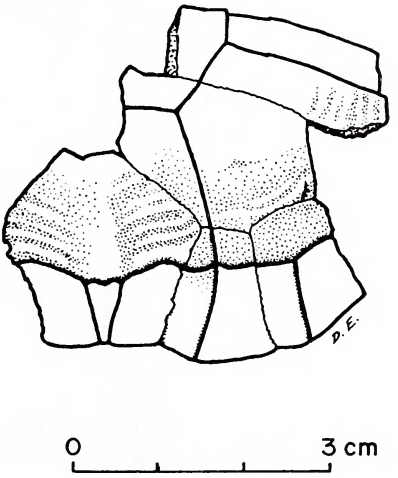
Isolated elements: 2 nuchals (.430-.431) ; 2 right epiplastra (.433-.434).

Characters used for identification: *C. muhlenbergii* fossils were distinguished from other emydid turtles based on characters listed in previous sections, along with additional nuchal and sulci characters given by Bentley and Knight (1993) (Fig.5).

Remarks: The soft bottoms and slow moving waters of swamps, bogs and marshes are typical aquatic habitats of the bog turtle (Ernst and Barbour 1989), but this turtle can also be found on land. *Clemmys muhlenbergii* has a patchy distribution in the Northeast, and ranges as far south as northern Georgia and extreme northwestern South Carolina. This disjunct spatial pattern has been interpreted as suggesting a larger former range (Smith 1957). The fossil evidence from the Ardis site suggests that the species' range extended at least 250 km farther southward during the late Pleistocene.

This is the second report of fossil material of *C. muhlenbergii* (Holman 1977) and represents the first fossil record from the eastern United States south of Allegany County, Maryland. This is the first sympatric occurrence of *C. muhlenbergii* and *C. guttata* in the fossil record.

Fig. 5 Partial fossil carapace of *Clemmys muhlenbergii* (.429). from the Ardis local fauna.



Terrapene carolina major- Gulf Coast Box turtle (Agassiz, 1857)

Material: An individual male specimen consisting of a partial carapace (SCSM 91.165.1) lacking it's anterior edge (Fig. 6), complete plastron (SCSM 91.165.2), partial skull (SCSM 91.165.19), 8 cervical vertebrae (SCSM 91.165.10-.17), 1 humerus (SCSM 91.165.5), both scapulo-acromial processes (SCSM 91.165.6-.7), both coracoids (SCSM 91.165.8-.9), complete pelvic girdle (SCSM 91.165.3), 1 femur (SCSM 91.165.4), 1 sacral rib (SCSM 91.165.18). An individual female specimen consisting of a complete carapace (SCSM 91.163.1) and plastron (SCSM 91.163.2), 2 cervical vertebrae (SCSM 91.163.10-.11), both scapulo-acromial processes (SCSM 91.163.4-.5), both coracoids (SCSM 91.163.8-.9), both femora (SCSM 91.163.6-.7), and complete pelvic girdle (SCSM 91.163.3). An individual female specimen consisitng of a complete carapace and plastron (SCSM 91.164.1-.2), 2 cervical vertebrae (SCSM 91.164.9-.10), 1 humerus (SCSM 91.164.8), 1 scapulo-acromial process (SCSM 91.164.4), both coracoids (SCSM 91.164.5-.6), 1 femur (SCSM 91.164.7), complete pelvic girdle (SCSM 91.164.3), and 1 caudal vertebra (SCSM 91.164. 11). An individual male specimen with complete carapace (SCSM 91.166.1) and posterior half of plastron from hinge (SCSM 91.166.2). An individual female spec-

imen consisting of a partial carapace and one half of posterior plastron from the bridge (SCSM 91.168.1). An individual female specimen consisting of a complete carapace and plastron (.435-.435.1). A individual partial carapace (SCSM 91. 167.1).

Isolated elements: 8 nuchals (.459-.466); 2 right 1st costals (.471-.472); 1 fused left 7th and 8th costal (.473); 5 costals (.474-.478); 3 left 5th peripherals (.479-.481); 2 fused peripherals (1 USNM) (1 UF); 32 peripherals (.510-.541)(2 USNM)(2 UF); 2 complete, 10 partial anterior plastral lobes (.467-.469)(6 USNM)(3 UF); 1 right epiplastron (.470); 2 entoplastra (.508-.509); 2 complete, 9 partial posterior plastral lobes (.507)(5 USNM)(5 UF); 32 large shell fragments (.510-.541); 1 partial skull (.436); 1 right maxilla (.437); 3 postorbitals (.438-.440); 4 mandibles (.441-.444); 3 cervical vertebrae (.456-.458); 4 humeri (.445-.448); 4 femora (.449-.451); 4 ilia (.452-.455).

Characters used for identification: The more complete specimens are easily separated from other emydid turtles based on their hinged plastra and overall morphology. *Emydoidea* differs from the box turtle by its smooth, unkeeled carapace and tends to be anteriorly constricted (Holman 1985).

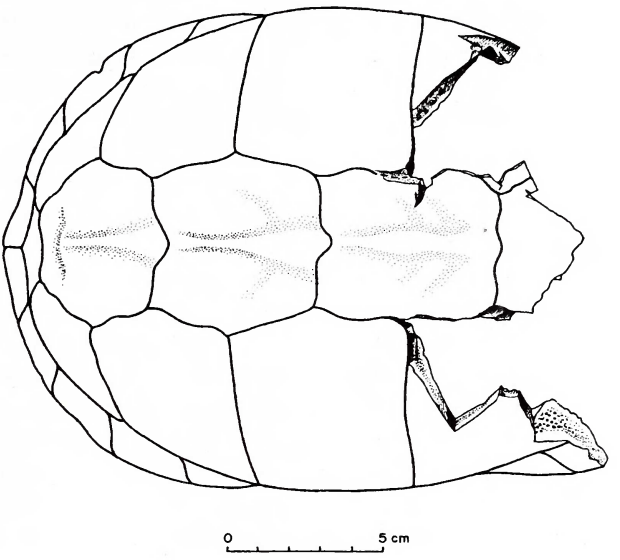
Plastron - The hinged plastral elements prevent confusion with any other emydid of North America except *E. blandingii*. The anterior end of this attachment area between the carapace and plastron differs from *E. blandingii*, as the carapace and plastron of *Terrapene* have a heavily sutured interlocking protrusion and pocket respectively. In *Emydoidea* this area lacks the sutured "ball and socket" mechanism and instead has a pronounced lateral flare generally located on the 5th marginal. The large size and robust nature of the fossil elements suggest an affinity to this subspecies.

Peripherals - These elements are distinguished by an upwardly curved anterior edge, forming, in some specimens, a "gutter-like" effect.

Humeri, femora, and ilia - Humeri and femora were separated from other emydid turtles based on comparison to Recent specimens and characters provided by Holman (1967, 1975). Ilia of *T. carolina* have a distinctive "boomerang-shape" and are straighter in other species (Holman 1977). Additionally, these fossil elements were identical to those retrieved from within the shells of the more complete fossil *T. c. major* collected from the Ardis site.

Remarks: This is the largest of the North American box turtles and today ranges from the coast of eastern Texas eastward along the Gulf coast into the Florida panhandle (Carr 1952). The Gulf Coast box turtle is commonly found in marshes, palmetto-pine forests, and upland hammocks. It enters water with a frequency similar to *T. c. carolina* (Carr 1952, Conant and Collins 1991).

Fig. 6 Partial fossil carapace of *Terrapene carolina major* (SCSM 91.165.1) which contained the skull (SCSM 91.165.19) shown in figure 6d.



Large fossil box turtle remains have generally been referred to as *T. c. putnami* or *T. c. putnami x major* (Milstead 1969). *T. c. putnami* differs from *T. c. major* only in size, attaining lengths upwards of 300 mm (Auffenberg 1967, Milstead 1969). The largest Recent specimen of *T. c. major* on record has a carapace length of 216 mm (Conant and Collins 1991). Auffenberg (1967) reported a large box turtle (233 mm), with skull, from Haile 8A, stating that it was very similar to *T. c. major*. Blaney (1971) placed *T. c. putnami* in synomyny with *T. c. major*, based on the shared characters of the two subspecies, and stated that size alone was not a justifiable reason to recognize a subspecies. The fossil box turtles from the Ardis site exhibit all the characters Milstead (1969) used to distinguish *T. c. putnami*. Furthermore, the five specimens had carapace lengths of 190.0 mm to 260.0 mm. Shell and axial elements of fossil box turtles from the Ardis site could not be consistently distinguished from Recent specimens of *T. c. major* except by size. Milstead (1969) stated that populations of *T. c. carolina* in Massachusetts and Michigan, on the northwestern edge of the subspecies range, appear to have strong morphological affinities to *T. c. major* having average carapace lengths of 140 mm and 139 mm respectively. Milstead suggested that this relationship may be due to a pre-Wisconsin influence of *T. c. putnami* or the influence of *T. c. triunguis*. An isolated, fused posterior plastral lobe (82.26 mm) collected from the Ardis site was estimated to belong to a specimen with a carapace length of about 140-145 mm. This plastral lobe might indicate the presence

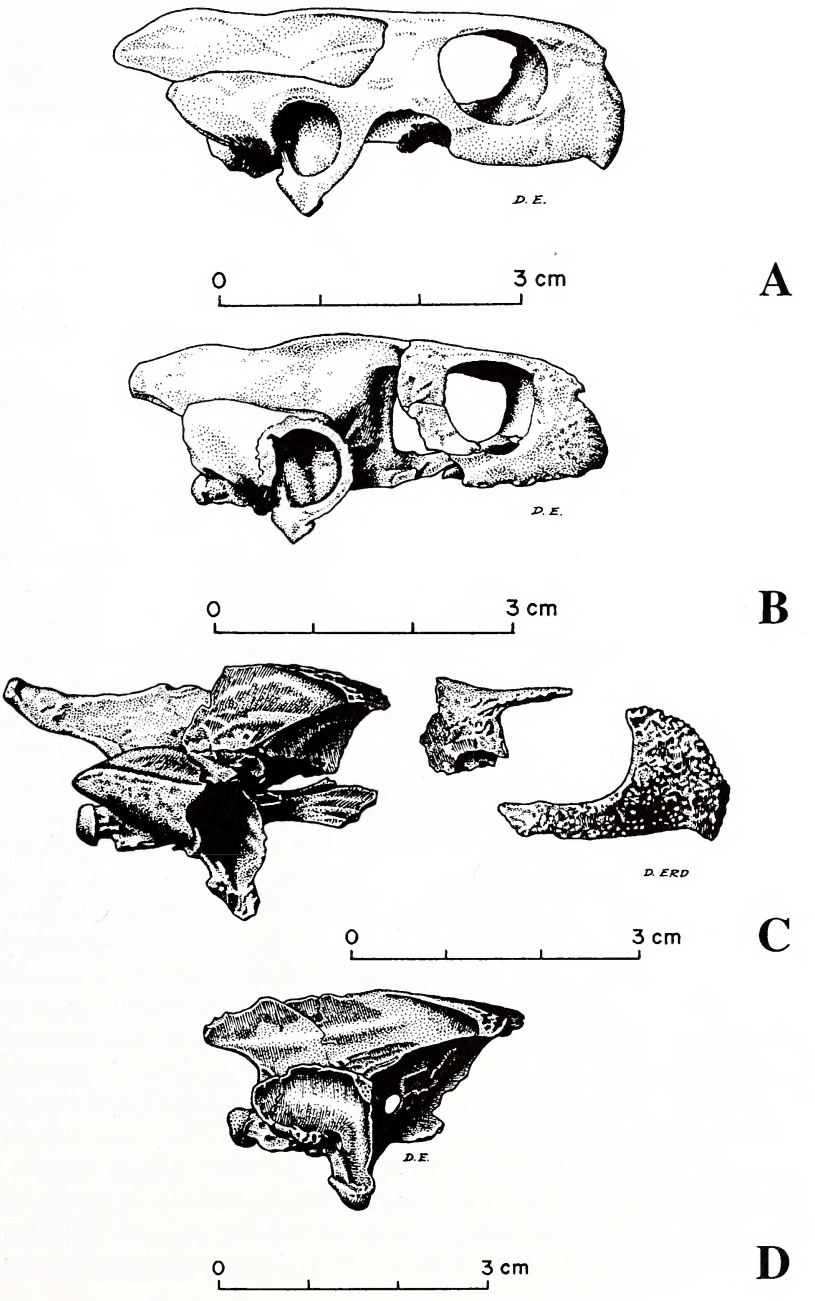
of box turtles at or near the size of the northwestern populations discussed by Milstead (1969). Additionally, several significantly smaller isolated peripherals were collected from the Ardis site, but these peripherals are largely unfused and may represent juveniles. The association of the smaller fused plastral lobe with significantly larger specimens suggests that during the height of the Wisconsin glaciation there may have been intergradation between local and northerly displaced populations of *T. c. carolina*, and populations of *T. c. major*, *T. c. triunguis*, and *T. c. bauri* radiating from the south. The Ardis population, being predominantly large box turtles, suggests that *T. c. major* traits (very large size, elongated shells, and upward curvature of peripherals) were more predominant during this time period.

The Ardis site produced two partial fossil skulls; SCSM 91.165.19 associated with a carapace of 245-250 mm. in length, and (.436), an isolated partial skull comparable in size to SCSM 91.165.19 (Fig. 6 and Fig. 7). We failed to distinguish any consistent differences between our skulls and Recent specimens except for size and an exaggerated upward curvature of the supraoccipital crest in specimen SCSM 91.165.19. This extreme curvature is considered an anomaly due to its complete absence in other fossil specimens; however, it is noted in Recent specimens but is less developed. The supraoccipital is thought to be one of the most variable cranial elements for box turtle systematics (W. Auffenberg, University of Florida, personal communication).

The parietals of most Recent specimens examined of *Terrapene carolina* had parietals that were inflated anteriorly, with a reduction in the tabled, dorsal surface of this element. Although extremely preliminary, we suggest a correlation between size and the degree of parietal inflation in *T. c. major*. Anterior inflation of the parietals is greatly reduced to absent among the largest specimens. In other subspecies of *T. carolina*, the inflation of the parietals remains fairly constant. The two skulls from the Ardis site do not exhibit anterior inflation of the parietals. The morphological similarities between the fossil box turtles of the Ardis site and the Recent and fossil specimens examined from museum collections (Fig. 7) suggests that the greatest affinity of the Ardis specimens is to *T. c. major*. They support the synonymy of *T. c. putnami* with *T. c. major* (Blaney 1971). Affinities noted by Milstead (1969) between northwestern populations and *T. c. major* may be a result of the proposed intergradation between box turtles during the height of the Wisconsin glaciation. The synonymy of *T. c. major* with *T. c. putnami* also suggests that *T. c. major* may have been capable of obtaining a considerably larger size than that observed in living specimens.

Although we believe a systematic revision of the genus *Terrapene* is needed, it exceeds the bounds of this faunal review. One of the goals of this discussion, however, is to emphasize the need for such a revision, based both on "standard" characters and on osteological characters of all fossil and extant forms.

Fig. 7 *Terrapene carolina major* skulls. A) Recent (UF 18963). B) Haile 8A (UF 3148). C) Ardis fossil (SCSM 91.165.19). D) Ardis fossil (.436).



Deirochelys reticularia - Chicken Turtle (Agassiz, 1857)

Material: 2 peripherals (.542-.543).

Characters used for identification: Identification is based upon the distinctive "spike-like" pattern of the dorsal sculpturing on these elements (Jackson 1964, Holman 1978).

Remarks: This turtle today has a continuous range from Texas and Oklahoma through the Gulf states and along the southern half of the Atlantic Coastal Plain states into North Carolina, with isolated populations in southeastern Virginia (Conant and Collins 1991). Still-water habitats, such as ponds, swamps, marshes, and temporary pools, are commonly occupied by chicken turtles, which reportedly do not favor moving water (Ernst and Barbour 1989).

This is the first fossil record of *Deirochelys* from South Carolina. The species most extensive fossil record and probable origin is in Florida (Jackson 1978).

Emydoidea blandingii - Blanding's Turtle (Holbrook, 1838)

Material: An individual specimen consisting of a complete carapace, anterior plastral lobe (.544), left lower jaw (.544.1), partial hyoid (.544.2), 1 partial humerus (.544.4), 1 partial scapulo-acromial process (.544.3), 1 femur (.544.5), 3 partial dorsal vertebrae (.544.8-.544.10), 1 ilium (.544.6), 1 pubo-pectineal process (.544.7), 1 sacral rib (.544.11). An individual specimen consisting of a complete carapace, 1 phalange, 2 partial vertebrae (UF). An individual specimen consisting of a nearly complete carapace, anterior plastral lobe, 4 partial dorsal vertebrae, 3 caudal vertebrae (USNM). An individual specimen consisting of a complete carapace, posterior plastral lobe (.545), 5 cervical vertebrae (.545.1-.545.5), 2 humeri (.545.21-.545.22), 1 ulna (.545.31), 2 scapulo-acromial processes (.545.27- .545.28), 2 coracoids (.545.25-.545.26), 1 dorsal vertebra (.545.6), 2 femora (.545.23-.545.24), 1 fibula (.545.29), 1 tibia (.545.30), 1 complete pelvic girdle (.545.20), 5 phalanges (.545.32-.545.35), 1 ungual (.545.36), 2 sacral ribs (.545.37-.545.38), 13 caudal vertebrae (.545.7-.545.19). An individual specimen consisting of a complete carapace and plastron, partial skull (2 maxillae, 1 quadrate, basioccipital-condyle, basisphenoid, frontal-postorbital-parietal skull fragment) (.546), partial hyoid apparatus (.546.2), 6 cervical vertebrae (.546.3-.546.8), 1 humerus (.546.20); 2 ulnae (.546.25-.546.26), 1 radius (.546.27), 2 scapulo-acromial processes (.546.28-.546.29), 2 coracoids (546.30-.546.31), 1 femur (.546.21), 1 tibia (.546.22), 2 fibulae (.546.23-.546.24), complete pelvic girdle (.546.19), 10 phalanges (.546.32-.546.41), 1 ungual (.546.42), 2 sacral ribs (.546.43), 10 caudal vertebrae (.546.9-.546.18). An individual specimen consisting of a complete carapace (.547). An individual specimen with the

anterior one half of the carapace (.548). An individual specimen with the anterior two-thirds of the carapace (.549). An individual juvenile specimen consisting of a partial carapace (nuchal, 1-2,4,8 neurals, pygal, 2-5, 7-11 left peripherals, 1-4 right peripherals, 3-8 right costals, 3rd left costal) and anterior lobe of plastron missing left epiplastron (.550), left xiphiplastron (.550.1), 1 dorsal vertebra (.550.2).

Isolated elements: 1 nuchal (.588); associated nuchal and 1st left and right costal with 1st left peripheral (USNM), 4 associated costals and single peripheral (.566); 1 left and 1 right 1st costal (.567-.568); 1 left 3rd costal (with rodent gnaw marks) (.569); 10 costals (.556-.565); 6 neurals (.570-.575); 3 right 1st peripherals (.576-.578); 1 left 5th peripheral (sub-adult) (.580); 1 left 6th peripheral (.579); 1 partial plastron (.607); 2 anterior plastral lobes (2 UF), 1 partial anterior plastral lobe (USNM), 2 pairs of associated epiplastra (.589-.590); 4 left and 2 right epiplastra (3 USNM)(3 UF), 7 entoplastra (.581-.587); 4 left and 6 right hyoplastra (.601-.602)(4 USNM)(4 UF); 4 posterior plastral lobes (.591)(1 USNM)(2 UF); 1 associated right hypoplastron and xiphiplastron (.592); 7 right and 8 left hypoplastra (.593-.600)(3 USNM)(4 UF); 3 right and 3 left xiphiplastra (.603-.606)(1 USNM)(1 UF); 2 partial skulls (.551-.552); 1 left postorbital (.553); 2 left auditory bullae and quadrate (.554-.555); 5 cervical vertebrae (.614-.618); 3 humeri (.608-.610); 3 femora (.611-.613); 1 partial pelvic girdle (.619).

Characters used for identification: It is possible to distinguish the more complete specimens of *Emydoidea blandingii* from *Deirochelys reticularia* on the basis of the hinged plastral elements and the lack of carapacial sculpturing in the former (Jackson 1978). Characters that distinguish this species from *Terrapene carolina* are given under that account. Isolated specimens can be distinguished from other emydid turtles based on characters mentioned in other sections of our paper and the following:

Epiplastron - *Emydoidea* epiplastron can be contrasted to *Terrapene* epiplastron in several ways. This element in *Emydoidea* differs from *Terrapene* by the presence of a depression located on the dorsal surface and medially to the anterior scute overlap area, which is less pronounced in *Emydoidea*. When compared to specimens of *Terrapene* of comparable size, this element is less robust and somewhat dorso-ventrally compressed. However, there is some difficulty in distinguishing large specimens of *T. carolina major* from *E. blandingii*. This element differs from *Trachemys* in that it is more elongated and thinner in *E. blandingii*.

Xiphiplastron - This element is most easily confused with *Clemmys*. Preston and McCoy (1971), suggested that the xiphiplastron of *Clemmys* is wider with respect to its length. Preston (1979) discusses additional characters used to identify this element in *Emydoidea*.

Neurals - These thin, very broad, smooth elements are distinctive among emydid turtles.

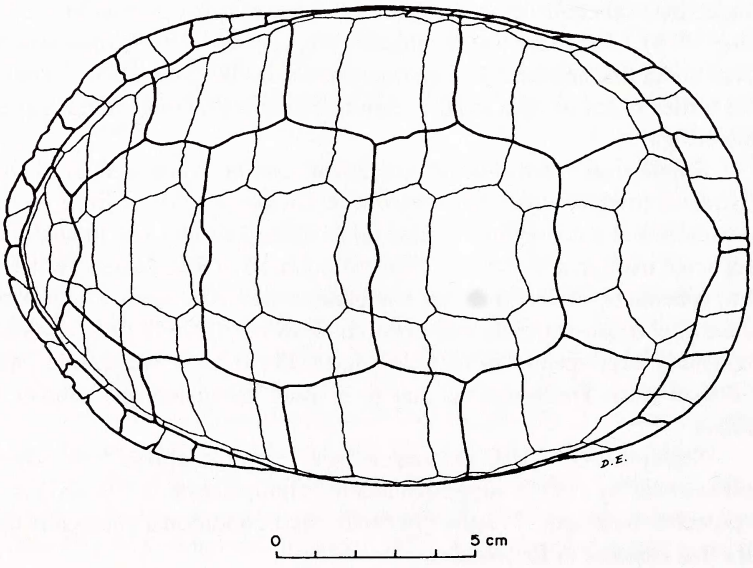
Axial and appendicular skeleton - Although cranial material of this species is distinctive, the generalized nature of the postcranial material makes the assignment to *E. blandingii* tentative.

Remarks: The recent distribution of *E. blandingii* is limited to southern Ontario and the Great Lakes region, with scattered populations occuring westward into northeastern Nebraska and south into northeastern Missouri, and eastward into New York and Massachusetts on the Atlantic coast (Conant and Collins 1991). The nearest fossil records of *Emydoidea blandingii* to the Ardis site are from Catalpa Creek, Mississippi (Jackson and Kaye 1975), and at New Trout Cave, West Virginia (Holman and Grady 1987). Both records are late Pleistocene.

The well preserved fossil material from the Ardis site (Fig. 8) is the first report of this species on the Atlantic Coastal Plain and is a range extension of about 1,200 km from its present continuous distribution and nearly 525 km south of the nearest reported fossil locality at New Trout Cave.

Habitats frequented by *E. blandingii* are generally in shallow, lentic waters with soft substrate, such as ponds, streams, marshes and sloughs (Ernst and Barbour 1989).

Fig. 8 Fossil *Emydoidea blandingii* carapace (.547).



Trachemys scripta - Slider Turtle (Schoepf, 1792)

Material: SCSM 91.169.1 a nearly complete carapace and plastron, partial right lower jaw, 1 scapulo-acromial process, 1 coracoid, 1 partial vertebra, partial pelvic girdle, 1 fibula. An individual specimen consisting of a partial carapace and plastron (.620).

Isolated elements; 3 nuchals (.621-.623); 23 partial costals (.624-.640)(3 USNM)(3 UF); 15 peripherals (.641-.655); 1 suprapygal (.656); 10 neurals (.657-.666).

Characters used for identification: This turtle is distinguished from other turtles by characters given by Holman (1985). Additionally, it has a diagnostic carapacial ornamentation.

Remarks: The slider has a nearly continuous distribution from Illinois southward into Texas and New Mexico and thence eastward across northern Florida north along the Atlantic coast into Virginia, with populations in Mexico and Maryland (Conant and Collins 1991). *Trachemys scripta* can be found in most freshwater habitats, but seems to prefer slow to non-moving water with a soft substrate (Ernst and Barbour 1989).

Today *Trachemys scripta* is common around the Ardis site and we have observed more than 10 within 100 m of the excavation site.

Pseudemys sp.-Cooters (Gray, 1855)

Material: 1 right 1st peripheral (.667); associated 9-10th right peripherals (.668); 2 peripherals (.669-.670).

Characters used for identification: These compare most favorably to species in this genus based on the thin, elongated sloping nature of the elements. We were unable to identify any diagnostic characters on these elements that could be used make a species placement. The only genus with which these may be easily confused is *Trachemys*. The fossil elements lack the sculpturing found in *Trachemys* and are significantly thinner and more elongated. The fossil peripherals also have a straight distal margin which contrasts with the notched margin in *Trachemys*.

Remarks: *Pseudemys* is a common genus of the Southeast, found in various aquatic systems (Conant and Collins 1991). The two species found in South Carolina today are *P. floridana* and *P. concinna*.

Testudinidae

Hesperotestudo crassiscutata -Giant Tortoise (Williams, 1950)

Material: 9 carapacial and plastral fragments (.671-.677)(1 USNM)(1 UF); 1 right xiphiplastron (.678); 1 vertebra (.685); 1 ungual (.686); 6 osteoderms (.679-.684).

Characters used for identification: The fragmented shell elements were assigned to this species rather than *H. incisa* on the basis of their extremely large size and robustness (40.0 mm thick). The large osteoderms, phalange, and vertebra could not be distinguished from *H. crassiscutata* in the Florida Museum of Natural History.

Remarks: Bramble (1971), Preston (1979), and Meylan (1995) place all North American non-*Gopherus* tortoises into the genus *Hesterotestudo*, and that practice is followed here. Dobie and Jackson (1979), provided the first report of (*Geochelone*) *H. crassiscutata* in South Carolina from the late Pleistocene of Edisto Island.

Trionychidae

Apalone sp.- Softshell turtle (Rafinesque, 1832)

Material: 1 partial nuchal (.47); 1 costal distal end (.48); 1 partial neural (.49).

Characters used for identification: These fossils are easily assigned to this genus, based on the relatively thin shell elements with characteristic pitting of the dorsal surfaces, general morphology, and the geographical distribution of Trionychidae. However, based on these elements, we were unable to identify a species with any certainty.

Remarks: Two species of the genus *Apalone* now occur in South Carolina, *A. ferox* and *A. spinifera*. Both species inhabit various aquatic environments with muddy or sandy bottoms in deep or shallow water (Ernst and Barbour 1989). *Apalone ferox* occurs throughout Florida and in the southern portions of Alabama, Georgia, and South Carolina. *A. spinifera* is restricted in Florida to rivers in the extreme northeastern and northwestern portions, and ranges no farther north along the Atlantic coast than North Carolina. It ranges westward into Colorado and north into Minnesota, with isolated populations in Montana, California, and

Mexico (Conant and Collins 1991). Only *A. spinifera* inhabits the area of the Ardis site today. Dobie and Jackson (1979) reported "*Trionyx* sp." from Edisto Island, South Carolina. Meylan (1987) has shown the correct name for North American softshells to be *Apalone*.

DISCUSSION AND PALEOECOLOGY

The turtle assemblage of the Ardis local fauna provides important new data for the late Pleistocene of the southeastern United States. In particular, it documents a shift in the spatial patterns of several turtle species during the late Pleistocene. The turtle fauna is unique in its geographical and temporal setting, and it contains the first sympatric fossil occurrences of several taxa, e.g., *Clemmys muhlenbergii*, *C. guttata*, *Emydoidea blandingii*, *Macroclemys temminckii*.

All of the fossil turtles collected from the site, except *Hesperotestudo crassiscutata* and *Terrapene carolina major*, are primarily aquatic and are commonly found in, or require, still or slow moving water with a soft substrate and aquatic vegetation (Ernst and Barbour 1989). Additional evidence of a nearby body of water included the presence of *Alligator mississippiensis* and elements of the fish fauna which are currently under study. This agrees with the habitat suggested by Bentley et al. (1994) based on the Ardis mammal fauna that indicates an ecotone between a mixed forest of conifers, hardwoods and meadows, and a permanent body of water such as a river or stream which may have given way to a bog or marsh. Portions of the mammalian fauna and avian material from the Ardis site further suggest the presence of a nearby large body of water such as a lake or pond. This association is based on the life histories and habitat requirements of many of the extant species represented in the Ardis fauna.

The Ardis turtle fauna consists of thirteen extant and one extinct species, with five taxa considered extralimital. Three of the five have northern affinities: *Emydoidea blandingii*, *Clemmys muhlenbergii*, and *Chrysemys picta*. *Terrapene carolina major* has a strong southern affinity. *Macroclemys* has a primarily Gulf coast distribution but extends as far north up the Mississippi Valley as Iowa (Pritchard 1989). Although *Hesperotestudo* was widespread in North America by the Miocene, Hibbard (1960) suggested that the presence of *Hesperotestudo crassiscutata* in a fauna indicated a mild climate with frost-free winters. The sympatric occurrence of species that are apparently ecologically incompatible today constitutes a "disharmonious fauna" (*sensu* Lundelius et al. 1983), which has been interpreted by many authors (Hibbard 1960, Holman 1980, Lindelius et al. 1983) as indicating a more equable climate (reduced seasonal temperature gradients) than that experienced in the region today. The Ardis local fauna reflects such a disharmonious biota, which clearly has no modern analogue. The turtle fauna corroborates conclusions made on the basis of the Ardis mammal fauna (Bentley et al. 1994), which also suggests that a more

equable climate than today prevailed near or during the maximum advance of the Laurentide ice sheet in the southeastern United States.

Based on the distribution of terrestrial vertebrates, Smith (1957) stated that the northeastern biota of North America was displaced southward during the Wisconsinan glacial maximum. Smith also suggested that during a "Climatic Optimum," southern counterparts dispersed northward. During the height of the Wisconsinan glaciation, *E. blandingii* would have been extirpated from its present-day northerly distribution (Mickelson et al. 1983, Conant and Collins 1991). The southern boundary of the Laurentide ice sheet, while abutted against the Appalachian Plateau (Mickelson et al. 1983), could potentially have forced the range of *E. blandingii* to be split, with one population occurring along the Mississippi Valley and another along the Atlantic Coastal Plain. This may have produced geographically isolated eastern and western populations of *Emydoidea blandingii* during the late Pleistocene.

In addition to *Emydoidea blandingii*, *Spermophilus tridecemlineatus* (thirteen-lined ground squirrel) was also collected from the Ardis site (Bentley et al. 1994). Based on Recent and fossil distributions (Kurten and Anderson 1980), the present northeastern distribution of the thirteen-lined ground squirrel also may have been displaced southward along the Atlantic Coastal Plain by the advancing Laurentide ice sheet.

As with the Gulf Coast Corridor, depressed sea levels during the Pleistocene glacial stage exposed much or all of the Atlantic continental shelf (Bloom 1983), thereby widening the Atlantic Coastal Plain. This may have facilitated the dispersal of glacially-displaced species southward along the coast. The newly emergent land area provided expanded habitats for species to utilize (Blaney 1971), and a more equable climate may have allowed for the range extention of both northern and southern species into these new areas. Northern populations of *T. c. carolina* in Massachusetts and Michigan that show affinity to *T. c. major*, discussed by Milstead (1969), may be relicts left over from a Pleistocene interval of extensive intergradation between the northerly displaced subspecies and radiating southern subspecies.

Bleakney (1958) suggested that the Recent population of *E. blandingii* in Nova Scotia survived glaciation in an "Atlantic Coastal Plain refuge" and then dispersed northward up the coast into Canada and Maine. Preston and McCoy (1971), suggested that "colonization of the Atlantic Coastal Plain from the Great Lakes region, along a 'steppe corridor' (Schmidt 1938) through the Mohawk Valley" was a more plausible hypothesis. Preston and McCoy (1971) also stated that the study of specimens from the eastern limits may provide an answer to the possibility of a "minor Atlantic Coast refuge for *Emydoidea* during ice advances." The presence of numerous *E. blandingii* at the Ardis site, as well as fossil material from New Trout Cave in West Virginia (Holman and Grady 1987), suggest that the Recent extreme northeastern populations may be products of a

re-invasion of the northeast by a substantial Atlantic Coastal Plain stock that had spread at least 900 km southward during the glacial advance of the late Pleistocene. Evidence from the Ardis local fauna indicates significant shifts longitudinally in the spatial distribution of *E. blandingii* along the Atlantic Coastal Plain during the late Pleistocene.

ACKNOWLEDGMENTS - We wish to express our gratitude to the staff of the Giant Cement Plant, Harleyville, South Carolina, for their generous cooperation, and in particular to Burt Ardis, for whom the fauna is named. Many thanks go to all the field volunteers: Vance McCollum, Linda Eberle, Craig and Alice Healy, Derwin Hudson, Ray Ogilvie, Lee Hudson, Tom Reeves, Martha Bentley, and Karin Knight. Robert Weems, U.S. Geological Survey, and Peter Meylan, Eckerd College, Petersburg, Florida, provided helpful discussion and review of this manuscript. We also wish to express our appreciation to Overton Ganong of the South Carolina State Museum; David Webb, Gary Morgan, and David Auth, of the Florida Museum of Natural History; Dennis Hermann, of Zoo Atlanta; and Greg Schneider, Museum of Zoology, The University of Michigan, and Justin Cougdon, Savannah River Ecology Labratory, Aiken, South Carolina, for allowing us access to their collections. Thanks go to Mike and Debi Trinkley, the Chicora Foundation, Columbia, South Carolina, for the use of their field equipment, and to Mike Runyon of Lander College, Greenwood, South Carolina, for donating fossil material for C14 dating. Darby Erd provided the illustrations.

LITERATURE CITED

Auffenberg, W. 1967. Further notes on fossil box turtles of Florida. Copeia 2:319-325.

Bentley, C. C., and J. L. Knight. 1993. The oldest spotted turtle: *Clemmys guttata* (Testudines:Emydidae), from the late Pleistocene (Rancholabrean) Ardis local fauna, Dorchester County, South Carolina. South Carolina Geology 36:59-63.

Bentley, C. C., J. L. Knight, and M. A. Knoll. 1994. The mammals of the Ardis local fauna (late Pleistocene), Harleyville, South Carolina. Brimleyana 21:1-34.

Blaney, M. R. 1971. An annotated check list and biogeographic analysis of the insular herpetofauna of the Apalachicola region, Florida. Herpetologica 27:406-430.

Bleakney, J. S. 1958. A zoogeographical study of the amphibians and reptiles of eastern Canada. Bulletin of the National Museum of Canada 155:1-119.

Bloom, A. L. 1983. Sea level and coastal morphology of the United States through the late Wisconsin glacial maximum. Pages 215-229 *in* Late-Quaternary environments of the United States (H.E. Wright, Jr., editor). University of Minnesota Press, Minneapolis. Volume 1.

Bowen, D. Q. 1988. A stratigraphic framework for multidisplinary work. Pergamon Press, Oxford, New York.

Bramble, D. M. 1971. Functional morphology, evolution, and paleoecology of gopher tortoises. Ph.D. Thesis, University of California, Berkeley. Library Photographic Service: Abstract.

Brett, C. E. 1990. Obrution deposits. Pages 239-243 *in* Palaeobiology: a synthesis. (E. G. Briggs and P. S. Crowther editors). Blackwell Scientific Publications, Oxford, England.

Brett, C. E., and S. E. Speyer. 1990. Taphofacies. Pages 258-263 *in* Palaeobiology: a synthesis. (E. G. Briggs and P.S. Crowther, editors). Blackwell Scientific Publications, Oxford, England.

Carr, A. 1952. Handbook of turtles. The turtles of the United States, Canada, and Baja California. Cornell University Press, Ithaca, New York.

Conant, R., and J. T. Collins. 1991. A field guide to reptiles and amphibians. Eastern and central North America. Hought Mifflin Company, Boston, Massachusetts.

Dobie, J. L., and D. R. Jackson. 1979. First fossil record for the Diamondback Terrapin, *Malaclemys terrapin* (Emydidae), and comments on the fossil record of *Chrysemys nelsoni* (Emydidae). Herpetologica 35:139-145.

Ernst, C. H., and R. W. Barbour. 1989. Turtles of the world. Smithsonian Institution Press, Washington, D.C.

Harris, W. B., and V. A. Zullo. 1991. Eocene and Oligocene stratigraphy of the outer Coastal Plain. Pages 251-262 *in* The geology of the Carolinas (J.W. Horton, Jr. and V. A. Zullo, editors). University of Tennessee Press, Knoxville.

Hibbard, C. W. 1960. Pliocene and Pleistocene climates in North America. Annual Report of the Michigan Academy of Science, Arts, and Letters 62:5-30.

Holman, J. A. 1964. Pleistocene amphibians and reptiles from Texas. Herpetologica 20:73-83.

Holman, J. A. 1966. Some Pleistocene turtles from Illinois. Transactions Illinois Academy Science 59:214-216.

Holman, J. A. 1967. A Pleistocene herpetofauna from Ladds, Georgia. Bulletin of the Georgia Academy of Science 25:154-166.

Holman, J. A. 1975. Herpetofauna of the Wakeeney local fauna (lower Pliocene: Clarendonian) of Trego County, Kansas. Pages 49-66 *in* Studies on Cenozoic paleontology and statigraphy in honor of Claude W. Hibbard (G.R. Smith, and N. E. Friedland, editors). Papers on Paleontology Volume 3, University of Michigan, Museum of Paleontology, Ann Arbor.

Holman, J. A. 1977. The Pleistocene (Kansan) herpetofauna of Cumberland Cave, Maryland. Annals of the Carnegie Museum of Natural History 46(11):157-172.

Holman, J. A. 1978. The late Pleistocene herpetofauna of Devil's Den sinkhole, Levy County, Florida. Herpetologica 34:228-237.

Holman, J. A. 1980. Paleoclimatic implications of Pleistocene herpetofaunas of eastern and central North America. Transactions of the Nebraska Academy of Sciences VIII:131-140.

Holman, J. A. 1985. Herpetofauna of Ladds Quarry. National Geographic Research 1(3):423-436.

Holman, J. A. 1990. Vertebrates from the Harper site and rapid climatic warming in the Mid-Holocene Michigan. Michigan Academician 22:205-217.

Holman, J. A., and F. Grady. 1987. Herpetofauna of New Trout Cave. National Geographic Research 3(3):305-317.

Jackson, C. G., Jr. 1964. The status of *Deirochelys floridana* Hay with comments on the fossil history of the genus. Tulane Studies in Geology 2:(3)103-106.

Jackson, C. G., and J. M. Kaye. 1975. The occurrence of Blanding's turtle, *Emydoidea blandingii*, in the late Pleistocene of Mississippi (Testudines: Testudinidae) Herpetologica 30:417-419.

Jackson, D. R. 1978. Evolution and fossil record of the chicken turtle *Deirochelys*, with a re-evaluation of the genus. Tulane Studies in Zoology and Botany 20(1-2):35-55.

Kurten, B., and E. Anderson. 1980. Pleistocene mammals of North America. Columbia University Press, New York, New York.

Lamb, T., and J. Lovich. 1990. Morphometric validation of the striped mud turtle (*Kinosternon baurii*) in the Carolinas and Virginia. Copeia 3:613-318.

Lundelius, L. E., Jr., R. W. Graham, E. Anderson, J. Guilday, J. A. Holman, D. W. Steadman, and S. D. Webb. 1983. Terrestrial vertebrate faunas. Pages 311-353 *in* Late-Quaternary environments of the United States (H. E. Wright, Jr., editor). Volume 1, University of Minnesota Press, Minneapolis.

Meylan, P. A. 1987. The phylogenetic relationships of soft-shelled turtles (Family Trionychidae). Bulletin of the American Museum of Natural History 186(1):1-101.

Meylan, P. A. 1995. Pleistocene amphibians and reptiles from the Leisey Shell pit, Hillsbourough County, Florida. Bulletin of the Florida Museum of Natural History 37 (9):273-297.

Mickelson, D. M., L. Clayton, D. S. Fullerton, and H. W. Borns, Jr. 1983. The late Wisconsin glacial record of the Laurentide ice sheet in the United States. Pages 311-353 *in* Late Quaternary environments of the United States. (H. E. Wright, Jr., editor). Volume 1, University of Minnesota Press, Minneapolis.

Milstead, W. W. 1969. Studies on the evolution of box Turtles (Genus Terrapene). Bulletin of the Florida State Museum 14(1):1-113.

Preston, E. R. 1979. Late Pleistocene cold-blooded vertebrate faunas from the mid-continental United States. 1. Reptilia: Testudines, Crocodilia. University of Michigan, Museum of Paleontology. Papers on Paleontology 19:1-53.

Preston, R. E., and C. J. McCoy. 1971. The status of *Emys twentei* Taylor (Reptilia: Testudinidae) based on new fossil records from Kansas and Oklahoma. Journal of Herpetology 5(1-2):23-30.

Pritchard, P. C. H. 1989. The alligator snapping turtle: biology and conservation. Milwaukee Public Museum, Milwaukee, Wisconsin.

Roth, J. A., and J. Laerm. 1980. A late Pleistocene vertebrate assemblage from Edisto Island, South Carolina. Brimleyana 3:1-29.

Schmidt, K. P. 1938. Herpetological evidence for the postglacial eastward extension of the steppe in North America. Ecology 19:396-407.

Smith, W. P. 1957. An analysis of Post-Wisconsin biogeography of the Prairie Peninsula region based on distributional phenomena among terrestrial vertebrate populations. Ecology 38:205-218.

Tushingham, M. A., and W. R. Peltier. 1993. Implications of the radiocarbon timescale for ice-sheet chronology and sea-level change. Quaternary Research 39:125-129.

Ward, L. W., B. W. Blackwelder, G. S. Gohn, and R. Z. Poore. 1979. Stratigraphic revision of Eocene, Oligocene and Lower Miocene Formations of South Carolina. South Carolina Geological Survey Publication. Geological Notes 23(1):2-32.

Webb, S. D. 1974. Introduction. 3-4 *in* Pleistocene mammals of Florida (S. D. Webb, editor). University of Florida Presses, Gainesville.

Received 3 January 1996
Accepted 13 August 1996

APPENDIX I
Taxa and Minimum Number of Individuals Present

Taxa	Minimum number of individuals
*Kinosternon subrubrum**	5
*Sternotherus odoratus**	4
Chelydra serpentina	3
*Macroclemys temminckii**	1
Clemmys guttata	19
*Clemmys muhlenbergii**	3
*Chrysemys picta**	25
*Deirochelys reticularia**	1
Trachemys scripta	4
Pseudemys sp.	1
Terrapene carolina major	12
*Emydoidea blandingii**	16
Hesperotestudo crassiscutata	1
Apalone sp.	1

Number of turtle species = 14
Number of individuals = 96
* = first fossil report from South Carolina